# Morphological Responses of Sugarcane to Long-Term Flooding

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## ABSTRACT

**Sugarcane (*Saccharum* spp.) in south Florida is often subjected to flooding due to intense summer rainfall or tropical storms. While there has been considerable research on the response of sugarcane cultivars to high water tables, there is a lack of information on cultivar morphological adaptation to long-term flooding. An experiment was established in Belle Glade, FL to examine: (i) effects of a July–September flood on the morphological characters of cv. CP 80-1743 and CP 72-2086 and (ii) significant flood × cultivar interactions that could be used to screen sugarcane germplasm. Sugarcane leaf, stem, primary root, adventitious root, and aerenchyma development were measured in the plant cane (2003) and second ratoon crops (2005). Morphological changes in response to flooding were similar in both years, with flooding leading to a 38% reduction in leaf weight, 4 to 15 times greater adventitious root development, 108% greater aerenchyma pipe extension, and 115% greater aerenchyma pipe diameter. Both cultivars responded to flooding by producing aboveground adventitious roots at the expense of belowground primary root biomass. A significant cultivar × flood interaction on aerenchyma extension and diameter was noted. Under nonflooded conditions, CP 72-2086 produced constitutive aerenchyma more than halfway up the stalk, whereas CP 80-1743 produced aerenchyma only 10% up the stalk. Aerenchyma development up the stalk may be a useful screening tool to identify flood-tolerance in sugarcane cultivars.**


SUGARCANE is an important economic crop in the tropics and subtropics due to its high sucrose content and increasing interest in its bioenergy potential. In Brazil in 2004, 14.4 billion L of ethanol were produced from sugarcane (Pessoa et al., 2005). Sugarcane in south Florida is often exposed to flooding during the summer months. Floods, particularly if prolonged, have the ability to negatively affect sugarcane yields (Berning et al., 2000).

There is evidence, however, of tolerance to flooding in Florida Canal Point (CP) sugarcane germplasm. Sartoris and Belcher (1949) reported that CP sugarcane clones survived a 105-d flood following two tropical storms in 1947. Differences in "nodal" (adventitious) root development were recorded among genotypes. Deren et al. (1991b) screened 160 CP clones for flood tolerance during a 5-mo flood (July–November) Several clones, including commercial cv. CP 72-2086, recorded sucrose yield reductions <30% in flooded compared to nonflooded conditions. The authors surmised that CP germplasm was inadvertently selected for flood tolerance due to tropical storms in the history of the breeding program, and concluded flood tolerance was present in modern CP clones. Glaz et al. (2002) recorded variability among commercial CP cultivars in tolerance to high water tables, and recommended screening of genotypes under high water tables. CP 72-2086 was not affected while CP 80-1743 yields were reduced 25% in the high water table treatment. Glaz and Gilbert (2006) found that 2-d periodic floods increased cane and sucrose yields in plant cane crops of CP 72-2086 and CP 80-1827, and Chabot et al. (2002) reported that sugarcane transpiration rates were maintained under high water tables in cv. CP 66-345. Glaz et al. (2004b) reported that periodic flooding and draining to water table depths of 16 to 50 cm did not affect sugarcane leaf photosynthesis.

Two common morphological changes of sugarcane in response to flood are the development of porous aerenchyma tissue ("piping") in the stalks and roots, and adventitious root development. Glaz et al. (2004a) measured aerenchyma development in CP sugarcane stalks and found constitutive aerenchyma (aerenchyma developed under nonflooded conditions) in CP 95-1429, which maintained yields over the growing season, despite repeated 7-d floods and extensive drainage. The authors surmised that constitutive aerenchyma development would be a useful adaptation for flood tolerance. They also found that flooding reduced yields of CP 95-1376, which did not possess constitutive aerenchyma (Glaz et al., 2004b). Van der Heyden et al. (1998) reported that all 40 CP genotypes studied possessed constitutive root aerenchyma. However, there were differences in the extent of aerenchyma development among clones.

Development of adventitious roots in response to flooding is thought to be a tolerance mechanism to increase root aeration that allows the plant to maintain root function during flooding (Kovar and Kuchenbuch, 1994). These aboveground roots tend to grow horizontally to remain near the water–air interface. Aerenchyma formation in adventitious roots in response to flooding has been reported in a range of wetland and dryland grass species (McDonald et al., 2002). Srinivasan and Batcha (1962) flooded 68 clones from *Saccharum* and related genera for 6 mo. Profuse adventitious root and aerenchyma development in tolerant clones was noted. Webster and Eavis (1972) noted a reduction in sugarcane leaf area during a 30-d flood. Additionally, sugarcane root systems developed a dense mat of aerotropic, small diameter roots when flooded. The authors theorized reduction in root diameter under

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**Abbreviations:** CP, Canal Point; EAA, Everglades Agricultural Area; EREC, Everglades Research and Education Center.

flood was caused by death of root tips and subsequent stimulation of lateral roots.

Sugarcane primary (belowground) root response to flooding was examined by Pitts et al. (1990) who reported that high water tables reduced sugarcane primary root dry weight and depth of rooting. However, Morris and Tai (2004) and Morris (2005) reported root dry matter was not affected by water-table depth from 0 to 30 cm which was established following 2 mo of growth. In a study comparing the response of three species to high water tables, sugarcane produced 3 to 14 times more belowground biomass than sawgrass (*Cladium jamaicense* Crantz) or St. Augustinegrass [*Stenotaphrum secundatum* (Walt.) Kuntze] under high water tables (Morris, 2005).

While there is reasonable evidence to indicate that some CP cultivars may tolerate high water tables and intermittent flooding, there is a lack of information on differences among cultivars in morphological adaptation to long-term flood. This information would be useful to sugarcane growers since increased intensity of tropical storms in the last few decades across many tropical and subtropical regions (Emmanuel, 2005; Klotzbach, 2006) have increased the incidence of flooding. Additionally, if gross morphological changes in stalk aerenchyma or adventitious root development were linked to flood tolerance, breeding programs could use these traits for field screening of germplasm. However, Sukchain and Dhaliwal (2005), in a study examining genetic correlation of sugarcane traits under flood, found that selection for adventitious root development may not increase sugarcane yield under flooding.

Our study had two objectives: (i) to determine the effect of a 3-mo summer flood on sugarcane morphological changes, including stalk aerenchyma and adventitious root development, in two commercial cultivars known to have different tolerance to high water tables, and (ii) identify significant flood × cultivar morphological interactions that could be used for screening germplasm tolerant to flood.

## MATERIALS AND METHODS

### Experimental Design

The experiment was planted on 27 Feb. 2003 at the University of Florida Everglades Research and Education Center (EREC; 26°39′ N, 80°38′ W) in Belle Glade, FL on a Lauderhill muck (euic, hyperthermic Lithic Haplosaprist) soil series. The experiment was conducted in a group of fields with pre-existing water control structures to isolate water-table treatments hydrologically (Deren et al., 1991b). The experiment was a 2 × 2 factorial in a split-plot arrangement in a randomized complete block design with four replications, with flood as the main plot and cultivar the subplot. Each subplot was 15.2-m long by four rows wide with 1.5 m between-row spacing.

The two cultivars used in this study, CP 72-2086 (Miller et al., 1984; tolerant) and CP 80-1743 (Deren et al., 1991a; not tolerant), were chosen based on previous reports of their different tolerance to high water tables (Glaz et al., 2002). Water tables were maintained at either a target height of 15 cm above the soil surface (flooded), or at natural hydrological levels (nonflooded). The flood treatment was imposed from 1 July through the first week of October each season, the seasonal period of greatest rainfall during which flooding is most likely to occur in the Everglades Agricultural Area (EAA). Table 1 shows water table levels from July to September during the study period for flooded and nonflooded treatments in the plant cane and second ratoon crops. The flooded treatment was maintained by pumping water into the fields throughout the flood period. Boards were installed in drainage ditches at the field outlets to maintain flood height at approximately 15 cm above the soil surface during flooding. Results are reported for the plant cane crop in 2003 and the second ratoon crop in 2005. First ratoon crop results are not included because the passage of Hurricanes Frances and Jeanne through the EAA in September 2004 flooded the nonflooded plots and thus made flood treatment comparisons impossible. While the 2004 hurricanes adversely affected the first ratoon crop, sugarcane plants recovered sufficiently after harvest to produce similar leaf area indices before initiation of the second ratoon flood (data not shown).

One water table logger (Model WL15, Global Water Instrumentation Inc., Gold River, CA) equipped with a submersible pressure transducer was installed in the center of each flood treatment plot. Installation consisted of inserting an access tube that was made from perforated PVC well-water pipe (5.1 cm diam.) through the muck soil to bedrock. The water table sensors were placed inside the access tubes until the bottom of the sensors touched the bedrock surface. Water table heights were monitored every 15 min. and daily averages were recorded beginning 1 July and ending 30 September each year. Average monthly air temperatures were calculated from 15 min air temperatures recorded 2 m above the soil surface at the EREC weather station <1 km from the experimental site. Cumulative monthly rainfall totals were also calculated from daily rainfall totals from the EREC weather station.

**Table 1. Air temperature, rainfall, and water table heights for the plant-cane (2003) and second-ratoon (2005) sugarcane crops at the Everglades Research and Education Center, Belle Glade, FL.**

| Month | Avg. air temp. | Total rainfall | Water table height (flooded) | Water table height (nonflooded) |
|---|---|---|---|---|
| | °C | cm | cm above soil surface | |
| | | | Plant cane (2003) | |
| Jan. | 13.8 | 0.7 | – | – |
| Feb. | 19.4 | 3.0 | – | – |
| Mar. | 23.0 | 10.6 | – | – |
| Apr. | 21.6 | 10.1 | – | – |
| May | 25.3 | 9.3 | – | – |
| June | 25.9 | 12.5 | – | – |
| July | 26.3 | 15.0 | 16.2 | −7.8 |
| Aug. | 25.9 | 16.3 | 12.9 | −10.3 |
| Sept. | 25.9 | 13.8 | 11.7 | −15.4 |
| Oct. | 24.1 | 2.9 | – | – |
| Nov. | 21.7 | 7.1 | – | – |
| Dec. | 16.5 | 1.9 | – | – |
| | | | Second ratoon (2005) | |
| Jan. | 16.7 | 1.7 | – | – |
| Feb. | 17.4 | 3.3 | – | – |
| Mar. | 18.7 | 12.7 | – | – |
| Apr. | 20.1 | 3.5 | – | – |
| May | 23.3 | 15.8 | – | – |
| June | 25.6 | 23.1 | – | – |
| July | 27.3 | 11.3 | 13.3 | −18.3 |
| Aug. | 27.0 | 14.2 | 14.8 | −13.6 |
| Sept. | 25.9 | 9.1 | 4.0 | −23.4 |
| Oct. | 23.5 | 23.8 | – | – |
| Nov. | 20.3 | 3.6 | – | – |
| Dec. | 16.7 | 0.7 | – | – |

### Morphological Measurements

Immediately on cessation of the 3-mo flood in plant cane (7 Oct. 2003) and second ratoon (4 Oct. 2005), four stalks per plot were cut at ground level and used for morphological measurements. Each stalk was measured separately, and the four independent stalk measurements were then averaged to obtain a mean value for each plot. First, the number of nodes from ground level to attachment of the top visible dewlap leaf was counted. Subsequently, the stalks were cut horizontally at the midpoint of each internode, and the extension of aerenchyma "piping" development (Glaz et al., 2004a) up the stem was recorded as the number of aboveground nodes with continuous piping from the base of the stalk. Pipe proportional extension ($P_e$) was then calculated as:

$$P_e = \frac{\text{No. of nodes with pipe}}{\text{Total number of nodes on stalk}} \quad [1]$$

Stalk diameter at the midpoint of internode 1 (starting at ground level) was measured once to the nearest 0.1 mm using calipers. The stalk was then cut in half at this point. Aerenchyma development at internode 1 was recorded via two methods. First, the 0 to 5 piping scale developed by Glaz et al. (2004a) was used to rate the extent of aerenchyma development at the base of the stalk subjectively. Second, calipers were used to measure the diameter of the approximately round aerenchyma tissue at the widest point to the nearest 0.1 mm. This diameter measurement was used to calculate cross-sectional area of aerenchyma at the base of the stalk using the formula for a circle. Pipe proportional area ($P_a$) was then calculated as:

$$P_a = \text{Pipe area (mm}^2\text{)/stalk area (mm}^2\text{)} \quad [2]$$

The number of nodes containing adventitious roots was counted from the base of each stalk. Adventitious roots were detached from the root band of each node separately using a razor blade, and dried at 65°C to constant weight to determine adventitious root dry weight for each node. Total plant adventitious root weight was calculated as the sum of adventitious root weight for all nodes. Leaf and stem tissue were then separated, the stems cut longitudinally, and both were dried at 65°C to constant weight to determine leaf and stem dry weights. Total aboveground biomass per stalk was calculated as the sum of leaf + stem + adventitious root dry weight. These dry weights were also used to calculate dry weight ratios of leaf/stem, leaf/adventitious root, etc.

Belowground primary root samples were taken on 16 Dec. 2003 for plant cane and 8 Dec. 2005 for second ratoon. Three soil cores (3.8 cm diam.) at 0 to 15 and 15 to 30 cm depths were taken from the center rows at a distance of 2.5 cm from sugarcane stools. Within each soil depth and plot, the three cores were mixed to provide an aggregate sample. Belowground roots and soil collected were carefully washed on a 1 mm screen to remove soil. Remaining roots were scanned using WinRhizo-Pro (Regent Instruments, Sainte-Foy, QC, Canada) and analyzed for total root length, average diameter, projected surface area, and volume. Scanning resolution was 7.9 pixels $mm^{-1}$ using a flatbed scanner with a positive film transparency unit. Following scanning, root samples were dried at 65°C to constant weight to obtain root dry weight measurements for each plot.

### Statistical Analyses

Analyses of variance for all measurements were performed using the PROC Mixed statement in SAS, with replications as random effects and crop (plant cane or second ratoon), flood and cultivar as fixed effects. Least squares means statements were used to determine probabilities of significant differences among treatment means (Littell et al., 2002).

## RESULTS

### Climate and Water Tables

Air temperatures from July through September averaged 26.1°C (Table 1) during the plant cane crop and 26.7°C during the second ratoon crop. Total rainfall during the same period was 45.1 cm during the plant cane crop and 34.6 cm during the second ratoon crop. Average water-table height from July through September was 13.6 cm above the soil surface for the flooded treatment and 11.2 cm below the soil surface for the nonflooded treatment in plant cane, and 10.7 cm above the soil surface and 18.4 cm below the soil surface for flooded and nonflooded treatments, respectively, for the second ratoon crop. Water-table levels in the nonflooded treatments (11.2–18.4 cm below the soil surface) were generally higher than normally targeted for commercial sugarcane production (45 cm) due to the shallow soil depth and hydrology of the experimental site. However, a water table difference of 23 to 31 cm between flood treatments was maintained throughout the flood period (Table 1).

### Analyses of Variance

The 3-mo summer flood caused significant differences in aerenchyma pipe extension, pipe scale and diameter, leaf weight, adventitious root weight, total biomass, pipe area, proportional pipe area, and proportional pipe extension (Table 2). Significant differences between cultivars were noted for stalk length, pipe extension, pipe scale, pipe diameter, leaf weight, pipe area, pipe proportional area and pipe proportional extension. The interaction of cultivar × flood was significant primarily for aerenchyma characteristics including pipe extension, pipe scale, pipe area, pipe proportional area and pipe proportional extension. The effect of crop was significant only on stem weight and total biomass, which were greater in the plant cane than the second ratoon crop (data not shown). None of the interactions of crop and flood (crop × flood or crop × flood × cultivar) were significant for any of the morphological traits measured in this study (Table 2).

### Plant Growth

The 3-mo summer flood significantly reduced partitioning of photosynthates to sugarcane leaves (Table 3) in both the plant cane (37% reduction in leaf weight) and second ratoon crops (38% reduction). Leaf growth was visibly depressed in both years as flooded plants were yellow-green in color compared to greener nonflooded plants. Also, flooded plants had lower leaf/stem and leaf/total weight ratios, and tended to have higher stem/total weight ratios (Table 3). The higher stem/total weight ratio was due to lower leaf weights as stem weight was not significantly affected by flooding.

**Table 2. Analysis of variance *F* ratios and level of significance for morphological measurements.**

| Source of variation | df | Stalk length | Aerenchyma "pipe" extension | Stalk diam. | Pipe scale† | Pipe diam. | Stem wt. | Leaf wt. | Adv. root wt. | Total bio. | Pipe area | Pipe prop. area‡ | Pipe prop. extension§ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Crop (C) | 1 | 7.85 | 0.10 | 3.2 | 0.12 | 0.06 | 77** | 0.95 | 1.94 | 70.3** | 0.00 | 0.83 | 0.10 |
| Flood (F) | 1 | 1.12 | 25.9* | 0.65 | 34.1** | 21.4* | 8.13 | 75.6** | 60.5** | 25.7* | 42.3** | 39.5** | 29.9* |
| Cultivar (Cl) | 1 | 60.1*** | 60.4*** | 3.85 | 185*** | 265*** | 1.76 | 12.1** | 2.55 | 0.00 | 154*** | 153*** | 86.7*** |
| C × F | 1 | 7.41 | 0.4 | 0.25 | 0.68 | 0.08 | 2.78 | 0.09 | 6.85 | 2.42 | 0.04 | 1.03 | 2.51 |
| C × Cl | 1 | 5.7 | 1.2 | 11.7** | 1.77 | 7.1* | 0.22 | 0.34 | 1.20 | 0.07 | 3.95 | 0.08 | 1.56 |
| F × Cl | 1 | 0.0 | 16.2** | 0.33 | 10.9** | 2.88 | 0.01 | 1.80 | 1.43 | 0.31 | 29.6*** | 28.7*** | 13.1** |
| C × F × Cl | 1 | 1.3 | 0.02 | 2.21 | 0.59 | 0.37 | 2.12 | 1.50 | 2.25 | 0.72 | 0.78 | 0.77 | 0.03 |

* Indicates $P < 0.05$.
** Indicates $P < 0.01$.
*** Indicates $P < 0.001$.
† Subjective rating from 1 (no aerenchyma pipe present) to 5 (large aerenchyma pipe present).
‡ Defined as proportion of pipe cross-sectional area at base of stalk to stalk cross-sectional area (pipe area/stalk area).
§ Defined as proportion of pipe extension to stalk extension (no. nodes pipe/no. nodes stalk).

Cultivar CP 72-2086 had significantly greater leaf weights, leaf/stem, leaf/total and stem/total weight ratios than CP 80-1743 in both the plant cane and second ratoon crops. However, total plant biomass production was not significantly different between cultivars (Table 2).

Compared with the nonflooded treatment, flooded plants produced 15 times greater adventitious root weight in plant cane and four times greater adventitious root weight in second ratoon (Table 3). Differences between cultivars were not significant. Adventitious root development in response to flooding was noted up to node 4 in both cultivars (Fig. 1). Development of these roots at each node was similar between cv. CP 72-2086 and CP 80-1743 in plant cane (Fig. 1A). Adventitious root development was noted on average 15.5 cm up the stalk in plant cane and 19.5 cm up the stalk in second ratoon. Adventitious roots exhibited profuse growth in both cultivars at the water–air interface throughout the flooding period.

## Aerenchyma Development

Aerenchyma "piping" significantly increased with flooding. Pipe diameter at the base of the stalk increased by 116% in plant cane (from 3.8 to 8.2 mm) and 115% in second ratoon (from 3.9 to 8.4 mm) when flooded (Table 3). Subjective aerenchyma ratings using a pipe scale of 1 to 5 (Glaz et al., 2004a) recorded similarly large increases. Cultivar CP 72-2086 had pipes of larger diameter at the base of the stalk than CP 80-1743 in both the plant cane (88% larger) and second ratoon crops (56% larger).

Significant flood × cultivar interactions (Table 2) were noted for aerenchyma extension and diameter, and these results were consistent across plant cane and second ratoon crops. Aerenchyma pipe extended for an average >10 nodes for CP 72-2086 in both flooded and nonflooded conditions (Fig. 2A), however CP 80-1743 aerenchyma development was influenced by flooding, increasing from an average of 2.3 nodes under drainage to 11.8 nodes under flood. The ability of CP cultivars to produce aerenchyma under nonflooded conditions, termed "constitutive aerenchyma" has been noted as an important adaptive mechanism to produce acceptable yields under high water tables (Glaz et al., 2004a,b). Pipe extension as proportion of nodes in the stalk averaged approximately 0.75 for flooded CP 72-2086, 0.50 for flooded CP 80-1743 and nonflooded CP 72-2086, and 0.10 for nonflooded CP 80-1743 (Fig. 2B). Flooding led to aerenchyma development up the stem to nodes attached to green leaf tissue in CP 72-2086, but not in CP 80-1743. CP 72-2086 also produced greater aerenchyma cross-sectional area when flooded (Fig. 2C) which constituted a greater proportion of stalk area at the base (Fig. 2D). Aerenchyma tissue constituted 11 to 12% of basal stalk area in CP 72-2086 when flooded and 4 to 5% when not flooded, whereas CP 80-1743

**Table 3. Sugarcane morphological characteristics significantly affected by flood or cultivar in the plant cane or second ratoon crops.**

| Treatment | Pipe diam. | Pipe scale | Adv. roots | Leaf wt. | Leaf/stem | Leaf/total | Stem/total |
|---|---|---|---|---|---|---|---|
| | mm | 1–5 | g stalk$^{-1}$ | | g lf g stem$^{-1}$ | g lf g total$^{-1}$ | g stem g total$^{-1}$ |
| | | | | Plant cane | | | |
| Flood | | | | | | | |
| Yes | 8.2a† | 2.8a | 6.2a | 43.4b | 0.14b | 0.12b | 0.87a |
| No | 3.8b | 1.1b | 0.4b | 69.9a | 0.21a | 0.17a | 0.82b |
| Cultivar | | | | | | | |
| CP 72-2086 | 7.9a | 2.6a | 3.4 | 62.2a | 0.20a | 0.16a | 0.83b |
| CP 80-1743 | 4.2b | 1.3b | 3.2 | 51.1b | 0.15b | 0.13b | 0.86a |
| | | | | Second ratoon | | | |
| Flood | | | | | | | |
| Yes | 8.4a | 2.8a | 4.0a | 41.5a | 0.19b | 0.16b | 0.83 |
| No | 3.9b | 1.2b | 1.1b | 66.4b | 0.26a | 0.21a | 0.79 |
| Cultivar | | | | | | | |
| CP 72-2086 | 7.5a | 2.5a | 2.9 | 57.9a | 0.25a | 0.19a | 0.79b |
| CP 80-1743 | 4.8b | 1.5b | 2.2 | 50.0b | 0.21b | 0.17b | 0.82a |

† Means followed by different letters within the same column and treatment indicate significant differences between flood or cultivar treatment means ($P < 0.05$).

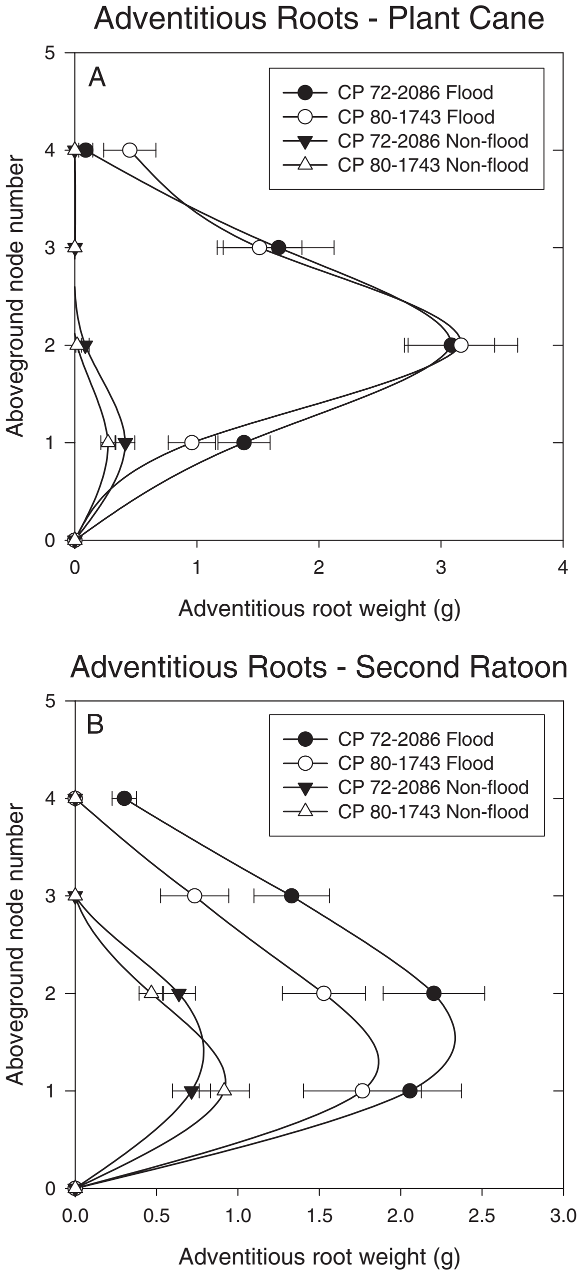


**Fig. 1. Adventitious root weight as a function of aboveground node number for sugarcane cv. CP 72-2086 and CP 80-1743 under flooded and nonflooded treatments in (A) the plant-cane crop and (B) the second-ratoon crop. Note the *x* and *y* axes have been reversed to graphically represent the development of adventitious roots on the sugarcane stalk. Error bars represent standard errors of the treatment means.**

aerenchyma accounted for 5% when flooded and only 1% when not flooded. In cutting each stalk longitudinally at each internode, we observed that aerenchyma piping tapered from the base of each stalk in an approximate cone shape. Applying the formula for a cone and using the proportional diameters and lengths of aerenchyma measured in this experiment, a total of approximately 2.8% of stalk volume was occupied by aerenchyma in CP 72-2086 when flooded, 1.0% in CP 80-1743 flooded, 0.7% in CP 72-2086 nonflooded and 0.05% in CP 80-1743 nonflooded. The ability of CP 72-2086 to produce longer pipes of larger diameter when flooded may be associated with constitutive aerenchyma development under nonflooded conditions.

## Primary Root Development

Significant differences in root dry weight, length, surface area and root volume were noted due to flooding in plant cane (Table 4). Cultivar and flood × cultivar effects on rooting traits were not significant in plant cane, nor were any significant differences noted in second ratoon due to high variability in root development (data not shown). In general, the 3-mo summer flood reduced all belowground rooting characteristics in plant cane due to significant reductions in the 0- to 15-cm soil layer. Flooding reduced root dry weight by 48%, root length by 29%, root surface area by 40% and root volume by 46% in the 0- to 15-cm layer.

## DISCUSSION

Our results indicate that a 3-mo summer flood reduced dry matter partitioning to sugarcane leaves and primary roots, while stimulating adventitious root and aerenchyma development in sugarcane cv. CP 72-2086 and CP 80-1743. CP 72-2086 produced more constitutive aerenchyma under nonflooded conditions, and aerenchyma pipes of larger diameter and volume than CP 80-1743 under flooded conditions.

Significant reductions in primary root growth in the plant cane crop in the 0 to 15 cm soil layer on flooding in our study do not concur with sugarcane root development reported previously under high water tables by Pitts et al. (1990) or Morris and Tai (2004). However, Morris (2005) recorded a nonsignificant decline in root dry weight of 35% in a high water-table treatment, compared with a 48% reduction in this study. Differences between our results and previous research may be due to long-term flooding above the soil surface in our study leading to a greater degree of primary root anoxia and death than would be expected with water tables at or near the soil surface.

One of the objectives of our study was to determine if gross morphological differences, suitable for field screening for flood tolerance in breeding programs, could be detected in sugarcane cultivars with different tolerance to high water tables. Morphological characteristics of interest include adventitious roots and stalk aerenchyma. Our study is the first to our knowledge to quantify adventitious root development in sugarcane stalks. Sukchain and Dhaliwal (2005) reported path coefficients of sugarcane germplasm and adventitious roots, but did not report adventitious root weights. Our results showed no significant difference due to flooding in adventitious root dry weight in two sugarcane cultivars with different expected flood tolerance. There were no statistical or visible differences in adventitious rooting, in contrast to the report of Sartoris and Belcher (1949) from sugarcane germplasm following the extended flooding in 1947. While this experiment included only two cultivars, subsequent field observations from

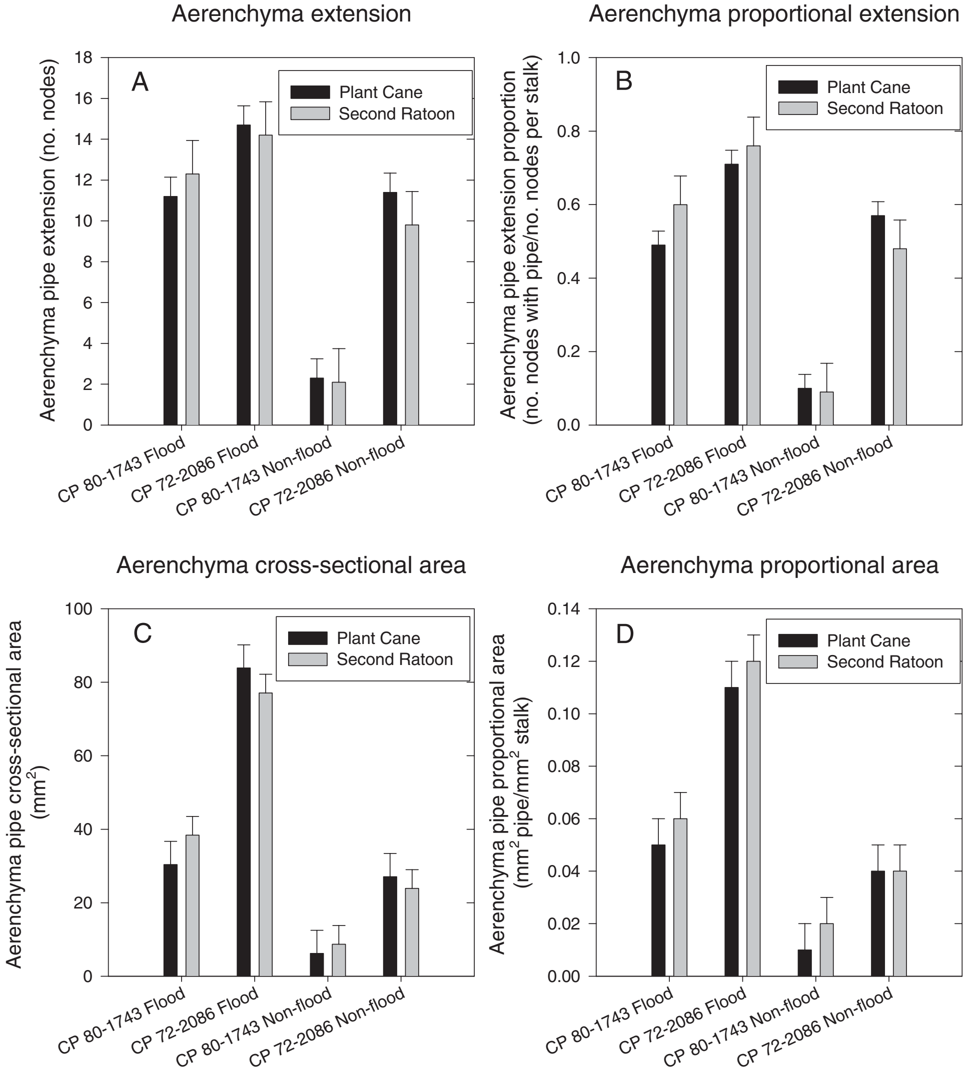


**Fig. 2. Effect of a 3-mo summer flood on sugarcane cv. CP 72-2086 and CP 80-1743: (A) aerenchyma extension, (B) aerenchyma proportional extension, (C) aerenchyma cross-sectional area and (D) aerenchyma proportional area in the plant-cane and second-ratoon crops. Error bars represent standard errors of the treatment means.**

partially-flooded sugarcane breeding Stage I (early-stage) fields of the CP program showed that all unique CP sugarcane individuals produced adventitious roots when subjected to short-term flooding. Our results with CP cultivars indicate that adventitious rooting ability would not be a useful screening tool to indicate sugarcane genotypic tolerance to flooding in sugarcane populations.

In contrast, our results indicate that constitutive aerenchyma development in the stalk may be an important indicator of flood tolerance. However, since this study included only two cultivars, follow-up testing with a large number of genotypes is recommended. Aerenchyma development was the only morphological characteristic that recorded significant flood × cultivar interactions on flooding, and aerenchyma development was consistent between the plant cane and second ratoon crops. There was good agreement between pipe diameter measured using calipers and aerenchyma development using the scale developed by Glaz et al.

**Table 4. Sugarcane primary root dry weight, length, surface area, and volume under flooded and nonflooded treatments in the plant cane crop.**

| | Dry wt. | | | Length | | | Surface area | | | Root volume | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | 0–15† | 15–30 | Total | 0–15 | 15–30 | Total | 0–15 | 15–30 | Total | 0–15 | 15–30 | Total |
| | g | | | cm | | | $cm^2$ | | | $cm^3$ | | |
| Flood | | | | | | | | | | | | |
| Yes | 0.41a‡ | 0.17 | 0.58a | 769a | 320 | 1090a | 141a | 64 | 205a | 2.12a | 1.04 | 3.17a |
| No | 0.21b | 0.12 | 0.33b | 546b | 304 | 851b | 85b | 56 | 142b | 1.15b | 0.86 | 2.02b |

† Refers to depth of soil sample (cm). "Total" = 0 to 30 cm.
‡ Means followed by different letters within the same column indicate significant differences between flood treatment means ($P < 0.05$).

(2004a), indicating that a subjective scale may be adequate for quantifying aerenchyma development at the base of the stalk. While Glaz et al. (2004a) noted constitutive aerenchyma development at the base of the stalk, this study is the first to our knowledge to characterize the extent of sugarcane aerenchyma development up the stalk. Quantifying the extension of aerenchyma development is important for two reasons. First, aerenchyma tissue which develops in nodes attached to green leaf tissue, as recorded for CP 72-2086 under flood, may provide a pathway for $O_2$ movement from the leaf stomates to the roots. Second, if constitutive aerenchyma developed more than halfway up the stalk in nonflooded conditions, as was also recorded for CP 72-2086, then this trait can be rapidly noted in the field by cutting one stalk per clone at its midpoint during field ratings. The CP sugarcane breeding program presently cuts one stalk from each stool (10,000 unique individuals) during early-stage selections. Clones with large pith or aerenchyma piping have until recently been discarded from the program. Our results are part of a growing body of work (Glaz et al., 2004a,b) on constitutive aerenchyma that indicate selecting for, rather than against, piping in the stalk may be advisable to identify sugarcane clones able to quickly adapt to flooded conditions. Since both CP cultivars tested developed constitutive aerenchyma at the base of the stalk, cutting the stalk midway rather than at ground level would be both faster and more appropriate for screening purposes. Geneticists that select against early stage sugarcane genotypes due solely to presence of aerenchyma risk discarding potentially high-yielding genotypes.

One reason clones with stalk aerenchyma have traditionally been discarded from sugarcane breeding programs is grower concern that aerenchyma or "holes" in the stalk represent stalk volume unable to store sucrose. Thus growers perceive that aerenchyma development represents lost profits. However, recent research indicating the importance of constitutive aerenchyma for high water table tolerance shows that presence of aerenchyma under nonflooded conditions is a positive trait for adaptation to high water tables. Our results indicate that approximately 4% of basal stalk area, or <1% of estimated total stalk volume, was occupied by aerenchyma cells in CP 72-2086 under nonflooded conditions. Growers will have to decide if this reduction in stalk storage capacity under dry conditions is worth the yield benefits constitutive aerenchyma may confer under wet conditions.

## CONCLUSIONS

A 3-mo summer flood reduced sugarcane partitioning to leaves and roots while stimulating adventitious root and aerenchyma development in both cultivars. However, a significant flood × cultivar interaction observed in aerenchyma diameter and extension indicates that constitutive aerenchyma development up the stalk in dry conditions may be a useful screening tool for sugarcane adaptation to flood.

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